Effect of Nitrogen Availability on Nitrogen Cycling in a Douglas-Fir Stand

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ABSTRACT. Short-term nitrogen cycling in a Douglas-fir stand was assessed for uptake and return to the forest floor. The five treatments included separate applications of nitrogen and carbohydrate, the latter being used to widen the forest floor C/N ratio and reduce N availability. Effects of nitrogen applications included increased N uptake and needle biomass and decreased forest floor weight compared to the control, while the carbohydrate treatment caused a reduction in N uptake, increased internal redistribution, and reduced needle biomass. FOREST SCI. 23:307–316.

ADDITIONAL KEY WORDS. Mineral uptake, litterfall, internal redistribution, fertilizers, *Pseudotsuga menziesii*.

THE GROWTH OF DOUGLAS-FIR (*Pseudotsuga menziesii* (Mirb.) Franco) stands of the Pacific Northwest has been shown to be limited by insufficient nitrogen since growth responses have been obtained from applied nitrogen (Gessel and others 1965, Heilman and Gessel 1963). Attempts to predict growth and nutritional responses and their magnitudes by use of foliage analysis have not met with much success (Cromer 1974).[1]

Forests are potentially capable of drawing on two sources of nutrients to maintain growth, one being the soil-humus complex and the other the internal reserves of the tree, the latter only being available to support growth in the short term. Field experiments on tree nutrition usually involve increasing the availability of a nutrient or nutrients in the soil, and monitoring tree responses and changes in tree nutrient status. This paper discusses the results of an experiment using an N deficient Douglas-fir stand in which N availability was increased and also in which attempts were made to decrease N availability below that encountered in untreated stands. The aim was to assess the magnitude and flexibility of the internal N reserves of Douglas-fir.

SITE AND METHODS

The study site was located in the University of Washington's Allen E. Thompson Research Center in the City of Seattle's Cedar River Watershed, 56 km southeast of Seattle. The climate is typical of the western foothills of the Cascades in Washington State at an elevation of 210 m. Climatic data was gathered at Landsberg approximately 3 km from the site. The average monthly temperature ranges from 1° to 18°C. Rainfall is approximately 130 cm with little snow but there is limited rainfall

[1] Cromer, R. N. 1974. Early response of unthinned Douglas-fir to urea in western Washington and Oregon. Internal Report for Regional Forest Nutrition Research Project, Univ Wash, Seattle. 45 p.

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TABLE 1. Summary of plot conditions prior to treatment and details of treatments in the experiment.

Treatment number	Mean dbh[a] (cm)	Stems/ha	Basal area (m^2/ha)	Treatment
1	15.5	2,133	37.2	Broadcast 880 kg ha^{-1} as urea.
2	15.5	2,000	34.9	Broadcast 220 kg ha^{-1} as urea.
3	14.7	2,267	35.6	Control.
4	14.9	2,041	34.6	Broadcast 8,000 kg ha^{-1} sucrose plus 10,000 kg ha^{-1} broadcast sawdust.
5	15.8	1,788	34.9	Broadcast 8,000 kg ha^{-1} sucrose, 10,000 kg ha^{-1} sawdust, 22 kg ha^{-1} P as superphosphate, and 110 kg ha^{-1} K as KCl.

[a] dbh = diameter at breast height over bark.

during three of the growing months. The soil is in the Everett series developed from the glacial outwash terraces formed about 12,000 years ago (Cole and Gessel 1968). This series belongs to the Brown Podzolic Group and is classified as a typic Haplorthod, coarse loamy over sandy, skeletal with mesic.[2]

The research center was located in a plantation of Douglas-fir which was established in 1931, planted at a spacing of 1.8 × 2.4 m, following a series of wildfires in the 10- to 20-year period after the logging of the original forest between 1910 and 1920. The principal understory species were salal (*Gaultheria shallon*, Pursh.), Oregon grape (*Berberis nervosa* (Pursh.) Nutt.), bracken fern (*Pteridium aquilinum* (1) Kuhn var *pubescens* Underw.), red huckleberry (*Vaccinium parvifolium* Smith), and a scattering of twinflower (*Linnea borealis* L. var *americana* (Forbes) Rehder). There were several species of mosses, the predominant species being *Eurynchium oreganum* (Sull.) Jaeg.

The aim of the experiment was to examine the short-term nitrogen cycling after nutrient manipulation. The experimental design involved five plots selected for uniformity, each of 0.023 ha (0.05 acre) with a 3 meter buffer strip. The treatments (Table 1) were an attempted gradation in N availability and ranged from hypothesized overabundance (880 kg/ha N) to stress conditions (carbohydrate applied to widen the forest floor C/N ratio). The carbohydrate consisted of 8,000 kg/ha sucrose broadcast plus 10,000 kg/ha sawdust broadcast. The sawdust was predominantly cedar (*Thuja plicata*) and chemical analyses indicated 0.09, 0.095, 0.092, 0.183, 0.110, and 0.017 percent of N, P, K, Ca, Mg, and Mn respectively.

Plots were square and established using a compass and tape. All trees in each plot were numbered by tags and the breast height diameter (dbh) taken to the nearest 0.13 cm (0.05 inches). An increment corer was used to take two cores per tree to estimate the previous five years' increment. The growth data obtained was used to estimate initial stand biomass and increment using Dice's (1970) regression equation ("Cedar River Model") after first testing with eight additional trees sampled over a range of diameter classes. A Fortran IV program was written to calculate biomass in which allowance was made for biasing of the log-log transformation (Madgwick 1970). By annual remeasurement, mortality and current growth

[2] Schlichte, A. K. 1968. The mineralogy of the Everett series soil on the Cedar River Watershed. M.S. thesis, Univ Wash, Seattle. 105 p.

were determined. Changes in foliage biomass after treatment were estimated by adjusting the biomass estimated from the regression equation using factors determined from changes in needle weights obtained from subsampling of branches (Turner and Olson 1976). Thus, for example, dry weight of current needles was found to be increased by 16 percent in the 880 kg/ha N treatment and the current needle biomass by regression was adjusted accordingly. The dbh change would be a poor indicator as diameter response may not occur until the second growing season. Litterfall weight was used to adjust total foliar biomass estimates and hence foliar biomass increased in the N treatments as a result of both increased weight of current foliage and lower loss in litterfall.

Three trees per plot were sampled every month to determine tissue nutrient concentrations. Samples were taken in the upper and lower crown and for each age class of needles. Bark, branch, and wood samples were taken from 6 trees per plot —the wood being divided into 1 year age classes back to 10 years old. Because of damage incurred at time of treatment (mainly trampling) the understory was ignored. Forest floor weights were determined using eight randomly located 613 cm^2 round cores per plot.

The selection of methods for the measurement of nutrient transfers was made so that the data would be comparable to previous studies (Turner and Singer 1976, Cole and others 1968, Turner and others 1976) and also for convenience considering the large quantity of data to be collected. Tree litter production was determined from four 46 cm × 46 cm (18 inch × 18 inch) litter traps located randomly within each plot and collections made on the 20th of each month. Previous studies at this site have used twelve traps per plot but based on that data it was decided that four traps would be sufficient for this study considering also the stand uniformity. After drying at 70°C the Douglas-fir needles in the samples were separated from other litter material.

Nutrients transferred by throughfall were estimated from three collectors per plot, consisting of 613 cm^2 round funnels fixed into 60 liter plastic barrels. There was a fine screen placed over the funnel to eliminate the accumulation of fine material in the solution. The screen mesh of the throughfall collectors was the same as that used for the litter traps so that material passing through the litter traps could be estimated from collection as throughfall. Precipitation input was collected as for throughfall but in a collector set out in the open. Stemflow was collected as described in Cole and Gessel (1968). All of these solutions were sampled monthly at the same time as the litter samples except in periods of high rainfall when samples were collected weekly. To monitor nutrient transfers in water percolating through the forest floor, three tension lysimeter plates per plot were installed as described in Cole and Gessel (1968).

Estimations of within tree nutrient transfers were made by mass balance as in Turner and Singer (1976) and Turner and others (1976). Several transfers need to be defined:

1. Nutrient content of current tissue (N_c) is the sum of the nutrients contained in the current foliage, branches, and wood. The current foliage biomass was estimated by subsampling as described earlier while wood was estimated from remeasurement (dbh). Current tissue could not be determined on bark and roots so this is a source of error, but was assumed to be standard in all treatments.

2. Redistribution (N_r) is the quantity of nutrients retranslocated within the tissues. Optimally this would be estimated by analysing the tissue when it was current, then when it was 1 year old, 2 years, etc. until it was returned to the forest floor. Because of time limitations, it was assumed in this study that the concentration of nutrients in the older tissue when it was current was the same as that of the present current

tissue, ignoring, in this study, annual variation. Changes in the concentration, as the tissue matures, are attributed firstly to leaching (N_t) and secondly to redistribution. Leaching is assumed only to occur from foliage (rather than twigs) and is probably an overestimate as it consists of, not only leaching, but surface washing and removal of particulate organic matter from the tree. Changes in wood and branch nutrient concentration as tissue matures are assumed to be all redistribution.

3. Current net uptake (N_{uptake}) is the nutrients removed from the soil humus complex and is calculated as the difference between current tissue nutrient content and redistribution (adjusted for leaching) as follows:

$$N_{\text{uptake}} = N_c + N_t - N_r.$$

Litterfall is important as a source of redistributed nutrients. Stemflow was not considered as a leaching loss, but rather only the washing of the outside of the bark (Mahendrappa and Ogden 1973).

Sample Preparation

Plant tissue samples from both the tree and forest floor were dried at 70°C, sorted into components, and where necessary, weighed. Samples for analysis were then ground in a Wiley mill (40 mesh) and stored in glass screw-top jars.

Water samples were filtered and stored temporarily in glass bottles at 2°C. One liter of water from each sample was digested with 2.5 ml sulphuric acid and 30 percent hydrogen peroxide and evaporated to 2.5 ml. This remainder was then made up to one liter with distilled water and a 100 ml subsample taken for total nitrogen analysis. Nitrogen content of samples was determined using a Technician auto-analyser 11353. Nitrogen analyses of plant material were determined using a micro-kjeldahl method (Jackson 1958).

Results

Biomass and Nitrogen Content Changes in Foliage.—The net changes that occur in a nutrient cycle arise from changes in the quantity or nutrient concentration of the organic matter (or water). The changes that arose from the treatments applied in the Douglas-fir stand were a result of both of these factors.

The method used to determine changes in foliage biomass was to adjust the base level biomass, which was calculated from dbh by regression, by the current needle weight changes and litterfall. Therefore, significant changes in total foliar biomass were based upon significant differences in the current foliage and litterfall rather than on the total biomass. On this basis, as discussed in Turner and Olson (1976), mean current needle dry weights were changed by 10, 15, −17, and −15 percent compared to the control for the 880 kg/ha N, 220 kg/ha N, carbohydrate, and carbohydrate plus fertilizer treatments respectively. From an analysis of variance of the data, the equivalent of 8 percent difference between the means was found to be highly significant. Hence, the N applications caused an increase in total foliage biomass during the first year after treatment, while the carbohydrate treatments decreased it (Table 2). These estimates were based on subsamples of current foliage and litterfall as stated in the methods. These changes occurred for several reasons. One was the observed increase in the size of the current needles and a possible increase in current needle number by lower bud abortion in the N treatments, and these two parameters decreased in the case of the carbohydrate treatments (Turner and Olson 1976). It was not thought that the number of needles per bud increased or decreased since the treatments were applied after bud initiation and the needles are initiated at that time. The second reason for total foliage biomass

TABLE 2. The nitrogen cycle for the first year in the various treatments which have been tabulated from left to right according to hypothesized decreasing nitrogen availability.

	Experiment treatment										
	880 kg/ha N		220 kg/ha N		Control		Carbohydrate		Carbohydrate plus P, K, S, Ca		
Component	Organic matter	Total N	Organic matter	Total N	Organic matter	Total N	Organic matter	Total N	Organic matter	Total N	SDBM[a] N content
Total foliage (kg/ha)	10,340	137	9,900	111	9,400	94	8,480	80	8,530	83	
leaf litter (kg/ha/yr)	1,290	11.2	1,710	13.0	1,880	14.1	2,390	14.3	2,425	16.4	1.7*
leaf wash (kg/ha/yr)		0.8		1.0		0.9		0.8		1.0	N.S.
Current tissue (kg/ha)											
foliage	2,550	37	2,530	32	2,200	22	1,790	19	1,870	18	
branch	540	4	510	3	470	2	520	4	490	3	
wood	5,850	9	5,600	8	5,300	7	3,400	3	3,100	2	
Total	8,940	50	8,640	43	7,970	31	5,710	26	5,460	23	
Redistribution (kg/ha/yr)											
foliage		−19.0[b]		7.2		10.0		16.4		15.4	
branch		2.4		1.2		1.0		2.4		2.0	
wood		3.6		4.0		3.0		3.6		3.7	
Total		−13.0		12.4		14.0		22.4		20.1	
Uptake (kg/ha/yr)		63		31		17		4		3	
Uptake/current tissue content (percent)		126		71		55		15		13	

[a] SDBM—Significant difference between means.
[b] Negative redistribution is accumulation.
* Significant at the 1 percent level.

change was the length of time of needle retention. The N application treatments decreased leaf litterfall, while such litterfall was increased by the carbohydrate treatments. Analysis of variance of the data showed the 880 kg/ha N and carbohydrate treatments were significantly different from the control and each other. There was no difference as a result of the added P, K, Ca, and S in the second carbohydrate treatment.

Together with the changes in biomass there were also changes in foliage N concentration and these are summarized in Turner and Olson (1976). The N applications increased the N concentration in all age classes of needles, while the carbohydrate applications did not appreciably change the pattern from the control. The concentration of N in fresh leaf litter showed that the treatments influenced litter N concentration, the N fertilizer increasing N concentration and the carbohydrate decreasing it. There was an observable difference in the composition of the litter

in that there was a higher proportion of green litter in the N treatments and this was more probably blown off by the wind rather than abscissed.

Nitrogen Transfers External to the Tree.—The transfers external to the tree (Table 2) included leaf litterfall and throughfall. The woody litterfall was not included as it mainly consisted of old branches and assumed not to be influenced, in the short term, by the treatments. The litterfall N content (kg/ha) decreased with increasing N application because, even though the litterfall N concentration increased, the mass decreased to a greater degree.

Throughfall N content (kg/ha) did not appear to be affected by the treatments, and hence leaching from the foliage was not a significant factor of the throughfall which was considered to be a washing of the outer surface of the foliage and twigs.

Internal Nitrogen Transfers.—As tree tissue increased in age the inorganic nutrient content changed. Foliage N concentration declined constantly with increasing needle age (Turner and Olson 1976) and usually decreased even further prior to abscission. This decline could be attributed to foliar leaching, but as shown by the throughfall the quantities leached (kg/ha) were insufficient to account for the decrease. Based on needle weights this decrease in N was an absolute decline so that it was more probable that the changes were a result of redistribution within the tree.

Redistribution was calculated by mass balance (rather than directly), this calculation being dependent upon the estimation of the current tissue nutrient content (Table 2). Calculations were based on the concentrations in the winter collection when maximum leaf elongation had occurred. At the time of maximum nitrogen concentration (spring), very little elongation had occurred in the current needles. The effect of nitrogen fertilization was to increase both current foliage and wood biomass while the carbohydrate treatment had the reverse effect. Branch biomass was apparently not affected, but this is a component which is difficult to estimate by allometric relations and for which the nutrient concentration is quite variable. The foliage was the main N source or sink, and hence errors in the wood or branch component (the least reliable component) may be less critical when calculating the general trend. There was more N redistribution in the carbohydrate plots and less in the N fertilizer plots, and in the case of 880 kg/ha N treatment, there was net accumulation of N. Compared to the control, uptake was increased by a factor of three in the case of the 880 kg/ha N and quartered in the carbohydrate treatments.

Forest Floor Changes

The biomass of the forest floor was determined prior to establishment of the experiment, but was estimated only in the control and N treatments 1 year after treatment. The estimate of forest floor biomass in the carbohydrate treatments was considered invalid as the presence of sawdust made sample sorting and interpretation very difficult. There was considerable variation between plots prior to treatments. Twelve months after treatment there were apparent decreases in the three measured treatments (7 percent decrease in the control plot, 18 percent in the 220 kg/ha N plot, and 32 percent in the 880 kg/ha N plot) (Table 3). The variability within the plots had increased after treatment and this may have represented differential decomposition. The decrease in the control plot may have been a result of annual variation of the forest floor or alternatively increased decomposition arising from disturbance during plot establishment and sample collection. Taking the control plot as a base line there was an apparent decrease of 11 percent in forest floor biomass in the 220 kg/ha N plot and of 25 percent in the 880 kg/ha N plot. In

TABLE 3. Biomass of the forest floor, by treatments.

Treatment	Biomass prior to treatment (kg/ha)	Biomass after treatment (kg/ha)
880 kg/ha N	28,700 ± 2,300	19,600 ± 6,100
220 kg/ha N	37,900 ± 5,100	31,100 ± 5,700
Control	30,900 ± 3,700	28,700 ± 6,200
Carbohydrate	28,600 ± 4,300	—
Carbohydrate P, K, Ca, S	32,600 ± 3,300	—

view of the variation after treatment, the data was considered an indication of the trend which occurred as a result of N application.

The C/N ratio in the forest floor of the carbohydrate treatments was 110–120 at the commencement of the experiment and had declined to 70–80 after 3 months. Typical N concentrations in solutions passing through the forest floor are shown in Table 4 for two sampling times at 5 months and 8 months after the commencement of the experiment. There was a high concentration of N at the time of the first sampling in the N fertilizer plots but this had been reduced dramatically at the later sampling. The N solution concentrations from the carbohydrate treatments were higher than the control at both these reported sampling times and this was typical of all sampling periods. These estimates of total N may not reflect available N, and probably, in the case of the carbohydrate treatments with soluble sugar moving through the plate in solution there may be rapid utilization of N by micro-organisms thus decreasing availability.

Discussion

The aim of this experiment was to assess specific changes in the nutrient cycle of a Douglas-fir stand when the availability of N was altered. The Douglas-fir stand was N deficient but this was largely overcome by the application of 220 kg/ha N while 880 kg/ha N gave a luxury supply. The carbohydrate treatment was used to widen the C/N ratio of the forest floor and rooting zone of the soil and thus stress the already deficient N, while the further addition of P, K, Ca, and S was used to unbalance the N further (Kelly and Lambert 1972).

In the short term, during the first 12 months after treatment, specific components (foliage) were considered to be more sensitive than in the longer term. Thus, while a response in wood growth may be detected in the first year after urea application, greater responses would be expected in the second and third years (Gessel and others 1965).

TABLE 4. Concentration of total nitrogen (ppm) collected—forest floor lysimeter plates.

Treatment	5 months after experiment commencement	8 months after experiment commencement
880 kg/ha N	50.0 ± 10.2	1.8 ± 1.3
220 kg/ha N	15.5 ± 6.3	0.6 ± 2.4
Control	0.5 ± 0.26	0.4 ± 0.1
Carbohydrate	0.7 ± 0.1	0.5 ± 0.1
Carbohydrate P, K, Ca, S	0.6 ± 0.2	0.8 ± 0.2

220 kg/ha N Fertilizer.—Sufficient fertilizer was applied in this treatment to overcome the existing N deficiency based on past experience for that site, and, when compared to the control plot, changes can be detected. Increased available N in the soil allowed an increased uptake of 14 kg/ha N (82 percent) based on aboveground components (it would probably be higher than this if roots had been taken into account). Increased uptake has involved decreased redistribution within the tree. This decreased redistribution mainly occurred in the foliage. The older foliage and abscissing needles appeared to be the main source of this N for redistribution but the treatment produced longer needle retention. Coupled with a greater mass of current needles, there was a 5 percent increase in total needle biomass in the first year after treatment. The increased N concentration in needles of all age classes increased foliage total N content by 19 percent. The longer needle retention time resulted in lower leaf litterfall (9 percent) in the first year, but the litterfall had a higher N concentration leading to an 8 percent decrease in returned N.

The reduced C/N ratio of the forest floor resulting from the N fertilizer application increased the decomposition rate leading to an effective reduction of 11 percent in the forest floor biomass. Part of this reduction was probably a result of the lower litterfall.

880 kg/ha N Fertilizer.—This treatment supplied excessive N to the system with an effect on uptake which could be considered as luxury consumption by the trees. Total aboveground N uptake increased by 270 percent over the control leading to increased accumulation of N in the tissue. Nitrogen redistribution became a negative figure in the tree foliage indicating that a high accumulation of N had occurred. Generally the trends established in the 220 kg/ha N treatment continued, but more intensively in the 880 kg/ha N treatment. It would be expected that the response to this application, either in the form of increased wood production or some other way, would continue for a much longer time than that of the 220 kg/ha N.

Carbohydrate Applications.—The application of carbohydrate to the forest floor had the reverse effect of the application of N fertilizer. When compared to the control, this wide C/N ratio material applied to the forest floor halved N uptake thus producing increased internal redistribution. The two carbohydrate treatments are discussed together in this respect as the added inorganic salts did not appear to have a significant additive effect.

Increased N redistribution, especially from the older needles, resulted in reduced needle retention time and this coupled with the smaller current needle biomass (16 percent lower than control) reduced total needle biomass by 9.5 percent. Needle nitrogen concentration was reduced only marginally in comparison to the control but even so, total foliar N content was reduced by 13.5 percent. Leaf litterfall and litterfall N content were increased by an average of 28 and 8.5 percent, respectively, over the control.

Comparison of All Treatments.—The treatments provided varying availability of N for uptake by trees, and have shown the flexibility of mature trees (45 years old) to obtain N from either the forest floor-soil complex and/or in the short term the internal reserves of the tree. The reduction of N availability by the application to the forest floor of wide C/N ratio material gives weight to the theories on immobilization of nutrients in the forest floor with increasing stand maturity (Tamm and others 1960, Weetman 1962, Heilman 1966, Viro 1967). In these situations it was hypothesized that on sites with marginal nutrient availability (especially in respect to N), litter which is low in N (i.e., with a wide C/N ratio) is returned to the forest floor and this takes longer to decompose, thus lowering the availability of N even further. The trees then translocate more N prior to litterfall thus exacerbating the problem. Thus on marginal sites progressive nutrient deficiency can develop. In

Scots pine plantations in England, Williams (1972) found significant quantities of N were immobilized in the forest floor, and treatments which increased the decomposition rate (discing, narrowing the C/N ratio, raising pH) made more N available for growth. Adams and Dickson (1973) found 20 percent more N immobilized in the forest floor of a poor quality spruce stand, a quantity considered sufficient to aggravate the already poor N regime.

The application of large quantities of wide C/N ratio carbohydrate material to the forest floor in this experiment indicated that N can be immobilized in the short term inducing N stress in the trees. This N stress can be partly overcome by internal translocation of N. In the long-term situation (the natural forest situation) where the low C/N ratio litter and slow decomposition rates are causing immobilization, the longer period of time involved would cause a slower rate of decrease in both foliar N contents and productivity.

The narrowing of the C/N ratio by urea application has caused increased decomposition rates (this may also be a pH effect) thus lowering the biomass of the forest floor. The other nutrients which would have been released for tree uptake by this increased decomposition indicate that a response to N fertilizer application could well be partly a response from other otherwise immobilized nutrients.

Lysimeter plates gave some indication of total N solution concentration in the soil. N fertilizer treatments significantly increased the N concentration in solution but so did the carbohydrate treatments. When considering the soluble sugar available for microbial activity, the total N in the solution from the carbohydrate treatments is probably a poor indicator of N available for tree growth.

The tree foliage, which is the component most affected in the first year after treatment, increased when N was applied or decreased when N was rendered unavailable (as in the carbohydrate treatment). It is known that the foliage biomass in these stands becomes fairly constant for a given site quality (Turner and Long 1975), so if the effect of the fertilizers was permanent (which is not probable in the case of the carbohydrate), the stands will probably have some of the described effects until the new stability level is reached. Thus the reduced leaf litter of the N fertilizer treatments will probably remain somewhat reduced until the foliage biomass stabilizes, at which time there may be litterfall higher than that in the control.

The extent to which internal redistribution has supplied the N requirements for growth in the carbohydrate plots is great but how long this can be maintained was not assessed because of the problems of maintaining the treatment.

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